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On the verge? Preferential use of road-facing hedgerow margins by bumblebees in agro-ecosystems

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1 **Abstract**

2 The global pollinator decline is commonly linked to modern intensive farming
3 practices, partly because excessive herbicide and fertilizer use is thought to reduce
4 pollinator food plant availability. This effect is particularly obvious across crop- /non-
5 crop boundaries, but no study has compared pollinator and food plant abundance on
6 adjacent crop- and roadside margins. We compared bumblebee abundance along 30
7 hedgerows in SW England; bordered either side by roads and arable fields (cultivated
8 with wheat, barley, oilseed rape, or beans). Total bumblebee abundance along roadsides
9 was over twice that observed on adjacent crop-facing margins, irrespective of crop type
10 and this general pattern was apparent for three of the five most common bumblebee
11 species, including generalist and specialist foragers. Both the total number of flowering
12 plant species and the floral abundance of three of the five most visited plants was also
13 higher on roadsides; minor variation between crops was localised and unrelated to
14 margin orientation. We conclude that organic farming may offer some advantages for
15 pollinator conservation since it reduces field margin exposure to agro-chemical inputs.
16 However, since conventional farming will remain central to global food production,
17 modifications to current practices (such as the use of wildflower strips) are needed and
18 may have ancillary benefits for pollinators by protecting arable margins from
19 disturbance and agro-chemicals. In addition, the fact that the roadsides were
20 demonstrably better habitats for pollinators and their food plants than field-facing
21 margins underscores the widespread suggestion that roadside verges should be utilised
22 more as a conservation tool to promote pollinator biodiversity.

23 **Keywords:** agricultural intensification - ecosystem services - environmental
24 stewardship schemes - field margins – pesticides - pollinators

25 **Introduction**

26 The global decline of many different insect pollinators is now well established and the
27 potential repercussions for crop and wildflower pollination widely discussed (Ghazoul
28 2005; Gallai et al. 2009; Potts et al. 2010; Vanbergen et al. 2013). The likely causes of
29 pollinator declines are numerous, but centre around habitat loss and fragmentation
30 (Goulson et al. 2005; Winfree et al. 2009), the direct and indirect impacts of pesticide
31 use (Brittain and Potts 2011; Whitehorn et al. 2012), and related implications for
32 immune-competence and increased susceptibility to disease (Cameron et al. 2011;
33 Whitehorn et al. 2011). Each of these factors can be linked to the recent, large-scale
34 intensification of agricultural production (Vanbergen et al. 2013). Although all insect
35 pollinator groups have been affected to some extent, bees and bumblebees (*Bombus*
36 species) in particular, are perhaps the most emblematic of the causes and likely
37 consequences of recent pollinator losses. Within the UK for example, three out of the 25
38 known *Bombus* species are now extinct and a further eight have experienced major
39 contractions in distribution and abundance (Goulson et al. 2005) and the UK situation is
40 mirrored globally (Goulson and Hanley 2004; Williams and Osborne 2009; Cameron et
41 al. 2011). The loss of any pollinator has potentially negative consequences for effective
42 ecosystem service provision (Ollerton et al. 2011), but by virtue of their ability to
43 pollinate a large proportion of crop plants and wildflowers, and do so in climatic
44 conditions that other pollinators cannot tolerate, bumblebee decline is of particular
45 concern in temperate regions (Goulson 2010).

46 Recognising that any attempt to halt or reverse bumblebee losses has to be achieved
47 within the context of highly-modified agricultural landscapes, and continued economic
48 and societal pressure to maximise food production, many contemporary conservation

49 options focus on modification to existing farming practices. Consequently the subsidy
50 of cultivated wildflower strips and low input pasture to increase food plant availability
51 became successful pillars of agri-environment schemes (Albrecht et al. 2007; Carvell et
52 al. 2007; Breeze et al. 2014). There are however, other ways in which modification of
53 current farming practices can support bumblebees. By virtue of providing a large and
54 concentrated floral resource, mass flowering crops such as oilseed rape (canola),
55 sunflowers, and beans attract and support bumblebees (Westphal et al. 2003; Hanley et
56 al. 2011; Stanley and Stout 2013). Organic farming is frequently associated with
57 increased bumblebee abundance, not only because of reduced toxicological impacts of
58 agro-chemicals on the insects, but also because of the associated increase in the
59 diversity and abundance of food plants (Belfrage et al. 2005; Holzschuh et al. 2007).
60 However, only a relatively small proportion of cultivated land is currently under organic
61 agriculture and the likely future contribution to global food demand is widely debated
62 (Connor, 2008; Seufert et al. 2012). The situation is complicated further as some authors
63 suggest that the link between organic farming and enhanced biodiversity may simply
64 reflect lower crop yield, since some high productivity organic systems appear to be no
65 more beneficial to wildlife than their conventional counterparts (Gabriel et al. 2013; but
66 see Tuck et al. 2014).

67 As the largest component of semi-natural habitats in Europe and North America
68 (Marshall and Moonen 2002), arable field margins are vital for maintaining bumblebee
69 populations. Even in the most intensively farmed systems, hedgerows, headlands, and
70 ditches provide at least some pollen and nectar forage in addition to opportunities for
71 nesting and hibernation sites (Mänd et al. 2002; Goulson et al. 2008; Hannon and Sisk
72 2009). Although found in many parts of NW Europe (e.g. the *Bocage* of Normandy),

73 hedgerows are particularly common in the British Isles and feature prominently in UK
74 conservation planning (e.g. Environmental Stewardship Schemes – see Merckx et al.
75 2009; Staley et al. 2012). There is concern however, that the range of agro-chemicals
76 routinely used in conventional farming impact severely upon the ability of arable field
77 margins to support biodiversity. Pesticide drift is a major problem, not only because
78 insecticides reduce bee survival and growth (Whithorn et al. 2012; Baron et al. 2014),
79 but also because of the negative impact on pollinator food plants (Marrs et al. 1989;
80 Schmitz et al. 2014). The use of inorganic fertilizers also has significant repercussions
81 for the composition of arable margin flora; elevated soil nitrogen levels promoting the
82 growth of highly competitive grasses at the expense of subordinate, herbaceous food
83 plants used by pollinators (Tsiouris and Marshall 1998; De Cauwer et al. 2006; Schmitz
84 et al. 2014).

85 In addition to providing habitat and corridors for biodiversity however, hedgerows can
86 also act as a filter for agro-chemical inputs. Tsiouris and Marshall (1998) report a
87 dramatic reduction in soil nitrogen concentration from the side of a hedgerow facing an
88 arable field to the opposite ‘control’ side, while Otto et al. (2009) show a similar effect
89 for pesticides. This effect is however, only likely to be apparent where one side of the
90 hedgerow does not routinely receive pesticide or fertilizer input, a situation most
91 commonly encountered when the arable field borders a road. Using this rationale,
92 Croxton et al. (2002) compared the plant and bumblebee communities either side of
93 hedgerows bordered by arable fields (wheat or oilseed rape) and green lanes (un-
94 metallated tracks used primarily by walkers and horse-riders). They showed that plant
95 species richness and bumblebee abundance were higher on the side adjacent to the green
96 lane, although they recognised that their results may have been partly confounded by the

97 fact that the central portion of the lane also contains pollinator food plants. Nonetheless,
98 similar variation in the abundance of bee food plants was reported by Henriksen and
99 Langer (2013) when they examined paired road and arable (wheat) margins in
100 Denmark. To date however, no study has compared bumblebee abundance across
101 hedgerows bordering sealed roads and arable fields containing multiple crop types.

102 The main aim of this study was to test the hypothesis that bumblebee abundance and
103 species composition vary across arable field - road boundaries, irrespective of the crop
104 being cultivated. Although disturbance and exposure to vehicular emissions might be
105 expected to have negative impacts on biodiversity (Forman and Alexander 1998;
106 Spellerberg 1998), many country roads experience relatively low traffic volumes and we
107 hypothesised that by virtue of the presence of hedgerows common in our study region,
108 road verges would offer enhanced forage opportunities for bumblebees. In addition,
109 there is a growing movement to use roadside verges as a means of promoting pollinator
110 habitat and abundance (Hopwood 2008; Noordijk et al. 2009; Wojcik and Buchmann
111 2012; Skórka et al. 2013) and our study offers a way of assessing the comparative value
112 of roadside verges for pollinators and their food plants.

113 **Materials and Methods**

114 *Study sites*

115 Bumblebee surveys were carried out over a 5-week period between early June and
116 early-July 2013 in 30 paired arable field and adjacent roadside margins situated in
117 Devon and Cornwall, southwest England (Table S1). All sites were situated amongst
118 intensively farmed, mixed arable and pastoral field systems typical of the region, and
119 were well away from other major land-use types (forestry, upland moorland) and major

120 urban conurbations (Plymouth, Torbay, and Exeter). Consequently, it is unlikely that
121 variation in land-use at the landscape-scale had any impact on bumblebee assemblages
122 around our chosen study sites. In addition all fields were between 50m and 190m absl
123 and we included a mixture of field and (crop-facing) margin aspects in our surveys such
124 that our observations were not biased by field/margin aspect or altitude (Table S1). All
125 margins were centred on long-established (i.e. > 200 years) hedgerows comprised of
126 several native woody plant species; e.g. *Corylus avellana* L., *Crataegus monogyna*
127 *Jacq.* *Fraxinus excelsior* L., *Prunus spinosa* L. *Rosa canina* L., *Rubus fruticosus* L., and
128 *Ulex europaeus* L. and which typically possess a naturally colonising, diverse basal
129 flora including *Dactylis glomerata* L., *Digitalis purpurea* L., *Geranium robertianum* L.,
130 *Heracleum sphondylium* L., *Ranunculus repens* L., *Silene dioica* (L.) Clairv., *Stachys*
131 *sylvatica* L., and *Urtica dioica* L. Typically both road- and field-facing hedgerows and
132 margins are cut once a year (in mid/late-summer) with little or no other deliberate
133 management. Consequently the trajectory of plant community development either side
134 of field boundaries likely reflects modification of a common basal flora by agro-
135 chemical input and disturbance on the field-side and (to lesser extent given low traffic
136 volumes) disturbance and exhaust fume emissions on the road-side.

137 While we were unable to ascertain a detailed account of pesticide use for study sites,
138 each land-owner confirmed that all arable fields had been in conventional cultivation for
139 several decades and were thus likely to have experienced a long history of exposure to
140 agro-chemicals. In addition, the structural similarity of the field margins, coupled with
141 the fact that all the arable crops we encountered are planted in rotation, means that crop-
142 type or associated agro-chemical application within individual farms were unlikely to
143 affect the location and abundance of bumblebee nests or hibernation sites, or plant

144 community composition. We focussed on four arable crops; wheat (*Triticum aestivum*
145 L.), barley (*Hordeum vulgare* L.), oilseed rape (*Brassica napus* L.) and field bean (*Vicia*
146 *faba* L.), which together account for 46%, 23%, 18% and 2% (by area) respectively of
147 all arable crops grown in the UK (Garthwaite et al. 2012). The use of replicate wheat
148 (9), barley (8), bean (7) and oilseed rape (6) fields also allowed us to compare whether
149 any variation in bumblebee assemblages between field- and roadside margins was
150 linked to crop type. All fields were separated by at least 1 km to minimize non-
151 independence of observed bumblebees (Knight et al. 2005; Osborne et al. 2008).

152 *Bumblebee surveys*

153 At each location we monitored bumblebee activity along a 100 × 2m transect set out
154 along the central part of an arable field margin, and matched this with an adjacent road-
155 side margin. UK agricultural policy requires a 1m border between the field boundary
156 and the crop edge, and for our arable fields this border was comprised primarily of the
157 perennial herb and grass species associated with the basal flora of the hedgerow. This
158 1m border, plus an additional metre extending to a point approximately half way into
159 the hedgerow proper, formed the 2m width of our transects on the arable field margin.
160 All adjacent road-side verges were selected such that 1m of verge was available running
161 from the hedgerow base to provide a mirror sample to the arable side.

162 Transects were walked once between 9:00-17:00 on days favourable to bumblebee
163 activity (Goulson and Darvill 2004). Each transect took approximately 15 minutes to
164 complete, with a 15 minute ‘rest’ period between sides to limit repeat sampling of
165 individual bees before the adjacent margin was sampled. We identified and recorded all
166 bumblebees observed actively foraging (i.e. actually visiting an inflorescence), together

167 with the plants upon which they foraged. Due to the difficulty of separating workers of
168 the subgenus *Bombus* s. str. (i.e. *Bombus terrestris* (L.), *B. lucorum* (L.), *B. magnus*
169 Vogt. and *B. cryptarum* (Fabricius) in the field (Williams et al. 2012), we made no
170 attempt to distinguish between these species and throughout refer to this group
171 collectively as *B. terrestris* agg. We made no attempt to capture foraging bumblebees,
172 but because transects were linear and completed relatively rapidly, it is extremely
173 unlikely that the same individual was recorded more than once during each transect
174 walk.

175 Immediately after completing bumblebee surveys, we estimated the number of flowers
176 of each plant species likely to be visited by bumblebees along each transect to determine
177 variation in floral resource availability between field- and roadside margins. Estimates
178 for total flower number were achieved by counting the number of flowers on 10
179 separate inflorescences of a given plant species and then to multiply this mean value by
180 the estimated total number of inflorescences observed along the transect. For Asteraceae
181 a capitulum was considered to be a single ‘flower’.

182 Following an Anderson-Darling test for normality and data transformation where
183 appropriate, we compared variation in total bumblebee visitation to road- and crop-
184 facing margins using a General Linear Model (GLM) with ‘margin orientation’ and
185 ‘crop’ as factors and the ‘margin orientation’ × ‘crop’ interaction to examine evidence
186 for crop-specific variation in bumblebee response to margin orientation. The same
187 approach was applied individually to each of the five most commonly visited plant
188 species. All analyses were performed in Minitab version 16.0.

189

190 Results

191 In total we observed 211 bumblebees foraging along hedgerow transects; the majority
192 of which (70%) were recorded on the roadside margin (Fig 1). We also observed some
193 variation between crops; barley field margins attracting on average over twice the
194 number of bumblebees (mean per transect = $4.9 \pm 0.8\text{SE}$) as beans (2.4 ± 0.3). A two-
195 factor GLM confirmed the strong effect of ‘margin orientation’ ($F_{1,52} = 27.7$, $P =$
196 <0.001) and ‘crop’ ($F_{3,52} = 4.42$, $P = 0.008$) on bumblebee abundance. However, there
197 was no ‘margin orientation’ \times ‘crop’ interaction ($F_{3,52} = 3.50$, $P = 0.458$), suggesting that
198 the higher abundance of bumblebees on roadside margins remained consistent for all
199 four crops.

200 The majority of forage visits were made by *B. terrestris* agg. (44.1% of total bumblebee
201 visits), followed by *B. hortorum* L. (16.6%), *B. pascourum* Scopoli (16.6%), *B.*
202 *lapidarius* L. (11.4%), *B. pratorum* L. (9.0%), and *B. hypnorum* (L.) (2.4%). A Chi-
203 square test of association found no significant difference ($\chi^2 = 10.58$, $df = 5$, $P = 0.06$)
204 in the relative frequency of the six *Bombus* species foraging on roadside or crop-facing
205 margins. Nonetheless, three species (*B. terrestris*, *B. hortorum* & *B. pratorum*) were
206 more frequent on the road-side margin with none of these yielding a significant ‘margin
207 orientation’ \times ‘crop’ interaction (Table 1).

208 A total of 22 different plant species were visited by bumblebees during the surveys and
209 on average more flowers of these species were available to bumblebees on roadside
210 verges than those facing the crop (Two-factor GLM: ‘margin orientation’ $F_{1,52} = 5.18$, P
211 < 0.027). However, neither the ‘crop’ ($F_{3,52} = 2.25$, $P = 0.094$) effect nor the ‘margin
212 orientation’ \times ‘crop’ interaction ($F_{3,52} = 0.71$, $P = 0.533$) were significant (Fig 2).

213 The five most frequently visited plant species were *Silene dioica* (38.4% of bumblebee
214 visits), *Heracleum sphondylium* (20.4%), *Geranium robertianum* (11.8%), *Digitalis*
215 *purpurea* (9.5%), and *Ranunculus repens* (9%), together accounting for 89% of all
216 recorded visits. Of these, the flowers of *S. dioica* (two-factor GLM on \log_{10} transformed
217 data - $F_{1,52} = 4.69$, $P = 0.035$), *G. robertianum* ($F_{1,52} = 16.35$, $P < 0.001$), and *R. repens*
218 ($F_{1,52} = 31.04$, $P < 0.001$) were more abundant on roadside margins (Fig 3). Two
219 species, *G. robertianum* ($F_{3,52} = 2.91$, $P = 0.043$) and *H. sphondylium* ($F_{3,52} = 4.78$, $P =$
220 0.005) exhibited variation linked to crop type, likely reflecting the high relative
221 abundance of the former in wheat margins and of the latter in barley. However, none of
222 the five species examined showed any ‘margin orientation’ × ‘crop’ interaction,
223 suggesting where plant species had higher floral abundance on roadside margins, the
224 effect was consistent across all crop types.

225 Discussion

226 Our results revealed that foraging bumblebees were more abundant along roadside
227 margins of arable field boundaries; an observation consistent for three of the most
228 common UK bumblebees and including species considered to be both generalist (*B.*
229 *terrestris* agg and *B. pratorum*) and specialist (*B. hortorum*) foragers. At the same time,
230 road-side margins offered more abundant floral resources for pollinators than the
231 adjacent crop-facing margin. Given the close relationship between forage plant
232 availability and bumblebee abundance (Heard et al. 2007; Hanley et al. 2014), it seems
233 reasonable to conclude that that the higher floral abundance on roadside margins was
234 responsible for elevated bumblebee numbers. Although we made no attempt to quantify
235 soil nitrogen or pesticide, a number of studies have shown marked variation in agro-
236 chemical concentrations just meters across arable field margins (Tsiouris and Marshall

1998; Croxton et al. 2002; Otto et al. 2009). It is likely that there was some deposition of nitrous oxides from car exhausts along our roadside margins, although recent evidence from North America (Bettez et al. 2013; Watmough et al. 2014) suggests that for even busy roads (i.e. a traffic volume of several thousand cars per day), annual roadside nitrogen deposition is at least two orders of magnitude lower than levels associated with agricultural inputs on crop-facing margins (Tsiouris and Marshall 1998). Consequently it likely that the across-hedgerow variation in flowering plant species abundance we observed for relatively low traffic volume countryside roads was linked to variation in soil nitrogen levels (see Tsiouris and Marshall 1998; De Cauwer et al. 2006; Schmitz et al. 2014), although additional impacts of herbicide application and disturbance (ploughing) are probable (Croxton et al. 2002). Indeed, Marrs et al. (1989) showed that the local effects of herbicide spray drift can be lethal for both *S. dioica* and *D. purpurea*, two of the most important bumblebee forage species observed in our study.

We also found remarkably little between-crop variation for either bumblebee or food plant abundance. Only *Bombus terrestris* agg exhibited any variation linked to crop type (being more abundant in barley margins) which may itself be explained in part by the higher relative abundance of *H. sphondylium* flowers. Like *G. robertianum* in wheat, where 35% of all recorded flowers for all crops were located along four hedgerows, 49% of all *H. sphondylium* flowers were recorded from five barley margins. Consequently the apparent concentration of *B. terrestris* agg on barley probably reflects local patchiness in forage availability rather than any variation due to the crop type itself (11 of the 18 observations of *B. terrestris* agg on *H. sphondylium* were from these sites). The fact that we found no ‘margin orientation’ × ‘crop’ interactions for individual bee or

261 plant species highlights the remarkable consistency in our results and corroborates our
262 conclusion that consistently higher floral abundance on roadside margins supported
263 more bumblebees, irrespective of the adjacent crop type.

264 Although Henriksen & Langer (2013) also showed that flowers of likely bumblebee
265 food plants were more abundant on the roadside margin of arable field boundaries, they
266 did not investigate the associated impact on the pollinator community. Croxton et al.
267 (2002) did report a positive association between plant and bumblebee communities
268 along track-sides, but their study focussed on green-lanes and investigated just two
269 different crop types (wheat and oilseed rape). Consequently ours is the first study to
270 show how (sealed) roadside margins support comparatively more bumblebees and their
271 food plants in comparison with adjacent crop-facing margins. This is important because
272 unlike green-lanes that offer forage resources within the lane itself, sealed roadside
273 margins offer a more robust control against which to compare the impacts of
274 conventional farming practices on the pollinator assemblages of arable field margins
275 (Croxton et al. 2002).

276 We recognise that we did not look at landscape- or even farm-scale impacts, but the fact
277 that bumblebee abundance varied so markedly between crop-facing and roadside
278 margins corroborates the widely-held view that conventional farming practices are
279 culpable (in this case via impacts on food plants) for recent pollinator losses (Goulson et
280 al. 2005; Brittain and Potts 2011; Cameron et al. 2011; Vanbergen et al. 2013). Farming
281 policy and practice is changing however. Recent schemes that encourage farmers to
282 cultivate or re-instate the flower-rich hay meadows required by many pollinators
283 (Goulson et al. 2005; 2006) are welcome, but when set against the global demand for
284 food, other options must be considered. Our results corroborate the view that by virtue

285 of reduced agro-chemical inputs (and noting that our design eliminates the potentially
286 confounding impacts of crop yield identified by Gabriel et al. (2013)), organic farming
287 could benefit the floral abundance of arable field margins and so promote forage
288 availability for pollinators. Nevertheless, any significant increase in the contribution of
289 organic farming to future global food supply remains in doubt (Connor 2008; Seufert et
290 al. 2012) and modifications to conventional farming methods seem the most likely way
291 to halt further pollinator losses. Due to the widening use of agri-environment schemes,
292 many such measures are already in place, but our results further underscore their
293 potential for pollinator conservation. Wildflower mixtures sown along arable field
294 margins are widely thought to benefit pollinators such as bumblebees by increasing
295 forage availability (Carvell et al. 2007; Pywell et al. 2011), but a further advantage is
296 that they provide a buffer against disturbance and agro-chemical input that may also
297 encourage pollinator-friendly plant species within the permanent field margin (see Kells
298 et al. 2001). Although these measures entail some loss of potential cropping area,
299 further benefits accrue to farmers if a minor reduction in crop yield is compensated by
300 increased pollinator service provision to crops (Breeze et al. 2014; Manning et al.
301 2014).

302 Our results also underscore the wider value of roadside verges for pollinator
303 conservation. Not only do roadsides provide refuge from intensive farming practices,
304 when taken together they offer considerable habitat potential; equivalent to over
305 236,000 Ha in the UK and over 3-million Ha in the USA (Wojcik and Buchmann 2012).
306 It is likely that even without any specific management, much of the available roadside
307 capacity in the UK already provides suitable pollinator habitat; this certainly seems to
308 be the case in our study. Moreover, it must be remembered that in addition to floral

309 rewards, in order for them to be attractive to bumblebees roadsides and adjoining areas
310 must also offer nesting and hibernation sites. Again, this is true of our field margins
311 since they were comprised exclusively of mature hedgerows. However, restoring
312 degraded or intensively managed (sub-)urban roadsides to encourage native, flower-rich
313 vegetation could benefit pollinator conservation particularly if nesting and hibernation
314 sites are available.

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467 **Figure Legends**

468 **Fig. 1.** Variation in mean (\pm SE) bumblebee abundance along 100m long
469 transects located either side of adjacent arable field margins (crop-facing versus
470 roadside). Observations were made along 100m hedgerow transects situated
471 next to one of four different crop types in 30 conventionally-farmed fields in SW
472 England.

473

474 **Fig. 2.** Variation in mean (\pm SE) abundance of all bumblebee forage plant
475 species along 100m long transects located either side of adjacent arable field
476 margins (crop-facing versus roadside). Observations were made along 100m
477 hedgerow transects situated next to one of four different crop types in 30
478 conventionally-farmed fields in SW England.

479

480 **Fig. 3.** Variation in mean (\pm SE) floral abundance of the five most frequently
481 used bumblebee forage plants along 100m long transects located either side of
482 adjacent arable field margins (crop-facing versus roadside). Observations were
483 made along 100m hedgerow transects situated next to one of four different crop
484 types in 30 conventionally-farmed fields in SW England.

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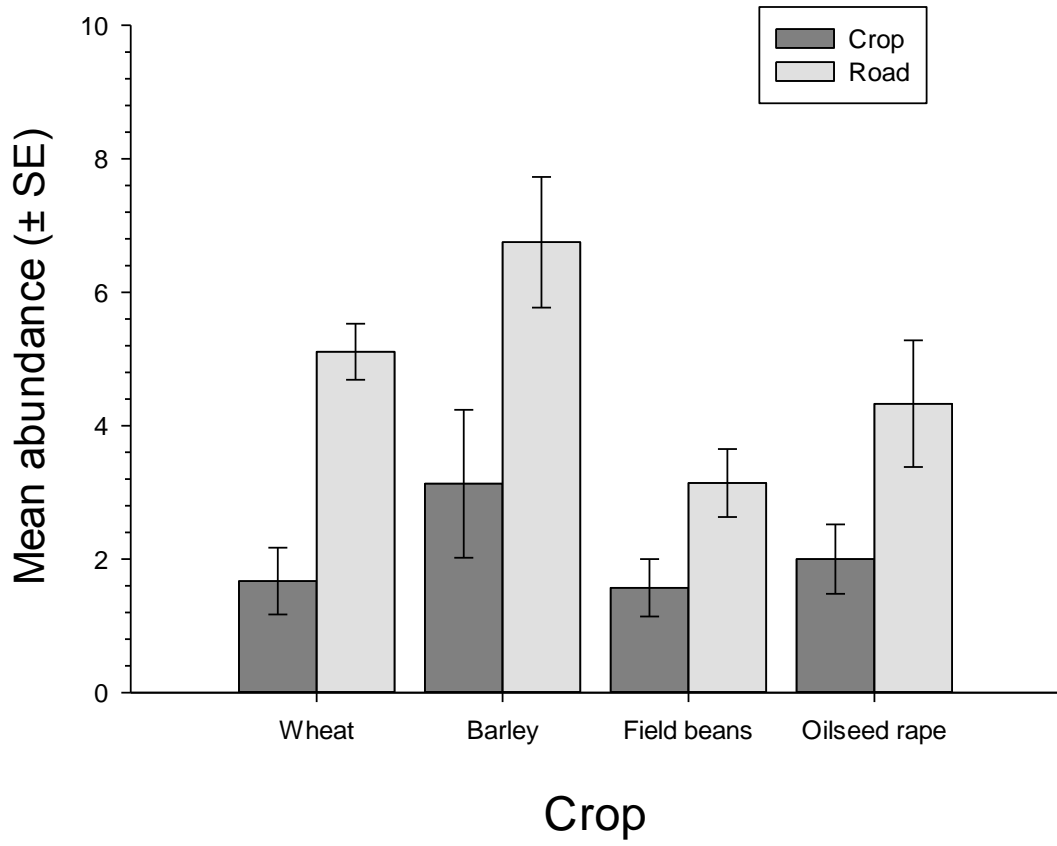
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488 Fig 1

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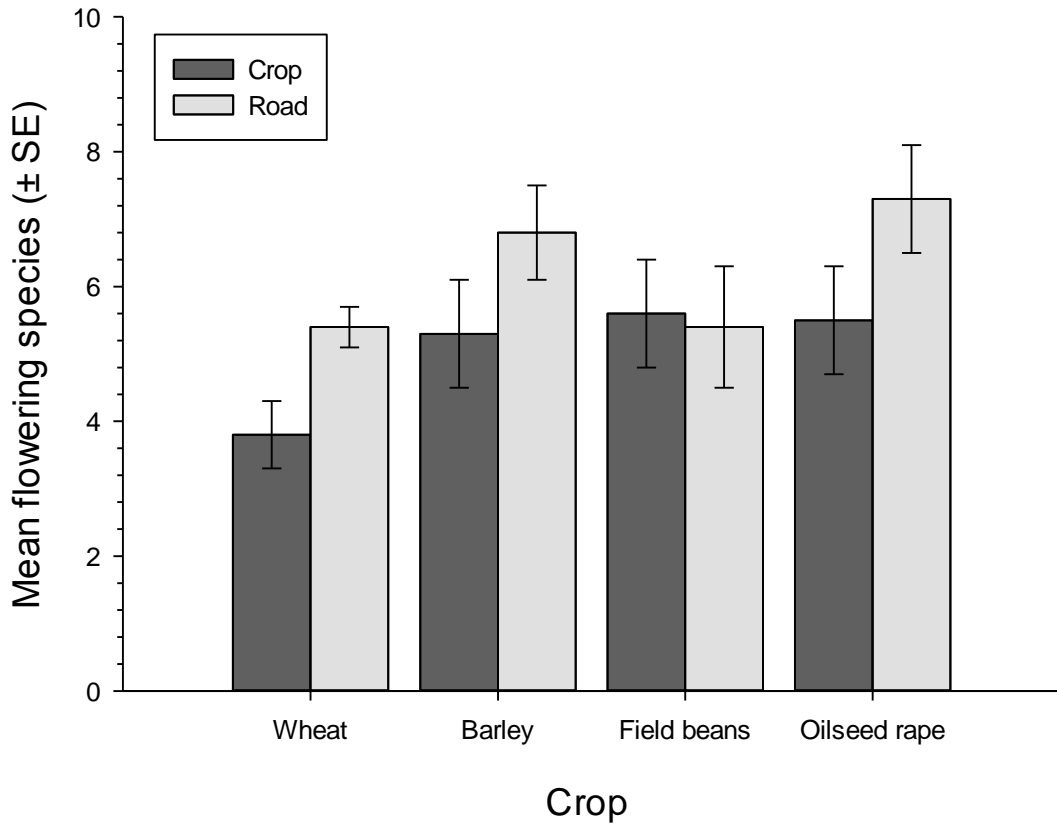
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501 Fig 2

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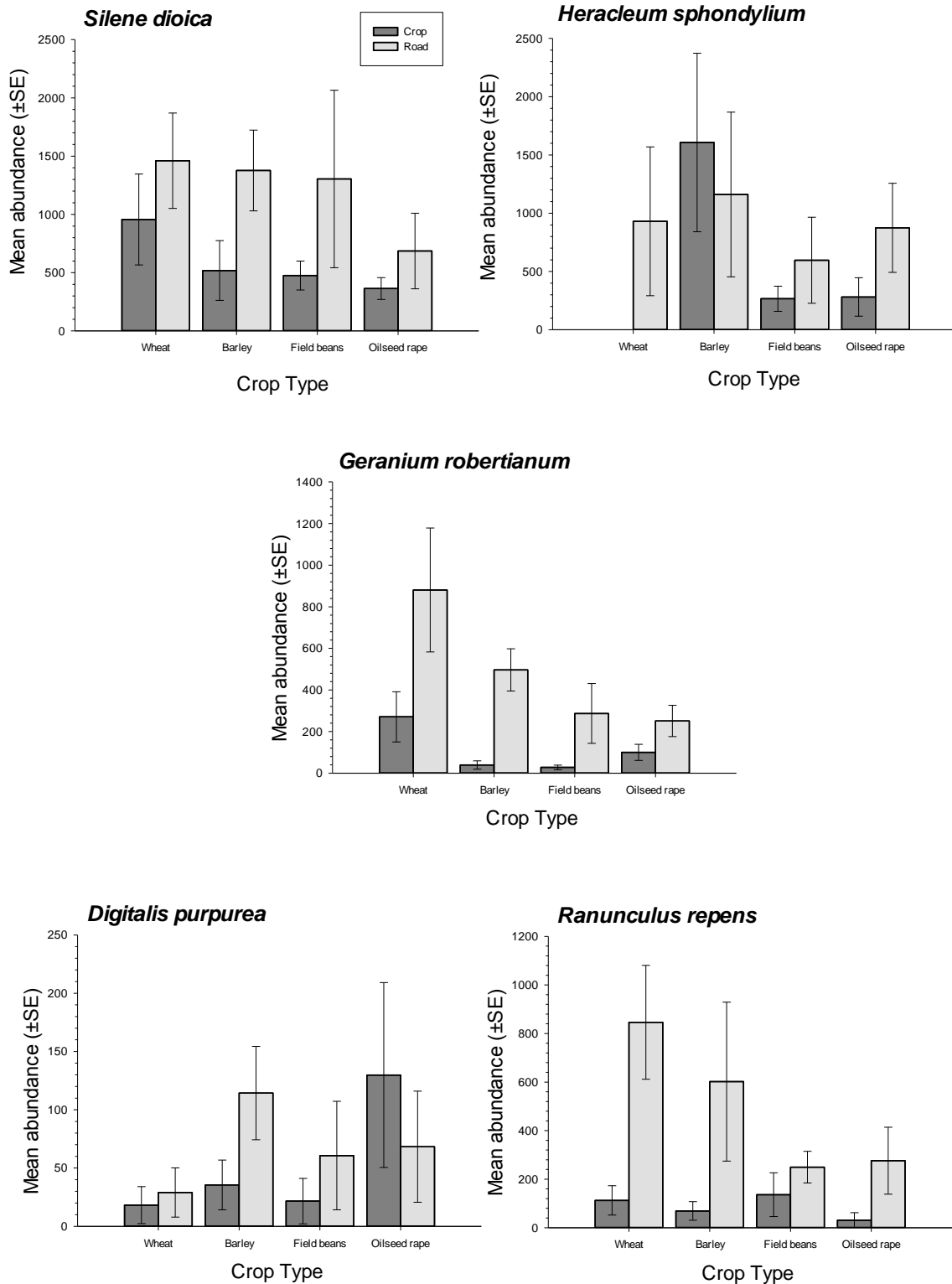


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506 Fig 3



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511 **Table 1.** Variation in mean (\pm SE) abundance of five bumblebee species observed foraging
 512 along adjacent 100m hedgerow transects either side of arable field margins (crop-facing versus
 513 roadside) situated next to one of four different crop types in 30 conventionally-farmed fields in
 514 SW England. Results of a two-factor General Linear Model examining the interactive effects of
 515 margin orientation and crop type are shown; emboldened '*P*'-values denote $P < 0.05$. In addition
 516 to the species shown, a further five individuals of *Bombus hypnorum* were recorded.

517

Crop	Margin orientation	<i>B. terrestris</i> (93 bees)		<i>B. hortorum</i> (35 bees)		<i>B. pascourum</i> (35 bees)		<i>B. lapidarius</i> (24 bees)		<i>B. pratorum</i> (19 bees)	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Wheat	Crop	0.78	0.43	0	0	0.33	0.17	0.33	0.17	0.11	0.11
	Road	1.78	0.28	1.00	0.29	1.33	0.41	0.67	0.24	0.33	0.17
Barley	Crop	1.38	0.53	0.50	0.27	0.75	0.41	0	0	0.25	0.16
	Road	3.63	0.56	1.38	0.42	0.75	0.41	0.71	0.34	0.38	0.18
Beans	Crop	0.86	0.26	0.14	0.14	0.43	0.20	0.14	0.14	0	0
	Road	1.43	0.20	0.29	0.18	0.29	0.18	0.14	0.14	0.83	0.44
Oilseed rape	Crop	0.83	0.31	0	0	0.17	0.17	1.00	0.37	0	0
	Road	1.50	0.56	1.33	0.76	0.33	0.21	0.33	0.21	0.83	0.31
All crops	Crop	3.22	1.04	0.56	0.24	1.44	0.47	1.11	0.31	0.33	0.17
	Road	7.11	1.02	3.33	0.71	2.44	0.60	1.56	0.18	1.78	0.52
GLM results		F	P	F	P	F	P	F	P	F	P
Orientation (DF = 1,52)		13.76	0.001	13.55	0.001	1.30	0.259	0.21	0.645	10.35	0.002
Crop (DF = 3,52)		4.93	0.004	1.81	0.157	1.64	0.192	1.91	0.140	0.32	0.812
Orientation \times Crop (DF = 3,52)		1.69	0.180	1.12	0.350	1.50	0.227	2.87	0.045	1.40	0.253

518